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Successional and seasonal changes of leaf beetles and their indicator value in a fragmented low thorn forest of northeastern Mexico (Coleoptera, Chrysomelidae)

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Abstract

Leaf beetles (Chrysomelidae: Coleoptera) constitute a highly diverse family of phytophagous insects with high ecological relevance, due to their host plant specificity and their close association to vegetation variables. Therefore, secondary succession and seasonal changes after loss of vegetal cover will have a significant influence on their community patterns. Accordingly, responses of leaf beetles to such environmental heterogeneity make them a suitable taxon for monitoring disturbance, which is more important for endangered habitats such as the low thorn forests (LTF) in northeastern Mexico. We conducted a study in a LTF fragment in order to assess the effects of secondary succession and seasonality on leaf beetle communities, as well as to quantify the importance of Chrysomelidae as an indicator taxon. Landsat scenes were used for delimiting a successional gradient, in which four succession categories were selected: four years, 17 years, and 31 years since loss of vegetal cover, and conserved areas. Eight plots of 100 m^2 were randomly delimited in each category; plots were sampled monthly, using an entomological sweep net, from May 2016 to April 2017. In total, 384 samples were collected by the end of study, from which 6978 specimens, six subfamilies, 57 genera, and 85 species were obtained. Species richness was higher in early succession areas. Abundance declined significantly from early successional to conserved areas, but the conserved areas had the higher diversity. Furthermore, differences in abundance were significant between rainy and dry seasons

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in areas of four, 17, and 31 years of succession, but not in conserved areas; also, all categories had a similar abundance during the dry season. Intermediate (17 and 31 years) and conserved areas differed in the season of higher diversity. Regarding inventory completeness, it was close to or above 70 % for all comparisons, although it was very low for the 17-year category during the rainy season. Faunistic similarity was higher between intermediate categories. A total of 24 species had a significant indicator value. Effects of succession time and seasonality on leaf beetle communities are here quantified for first time in LTF forests. Influences of environmental heterogeneity and intermediate disturbance are discussed as main drivers of the results obtained. Several leaf beetle species are proposed that could be useful for monitoring succession time and secondary LTF vegetation in northeastern Mexico. However, studies must be replicated at other regions, in order to obtain a better characterization of disturbance influence on leaf beetles.

Keywords

Chronosequence, community patterns, disturbance, seasonality, secondary succession, phytophagous beetles

Introduction

Chrysomelidae is the third most diverse family of Coleoptera in the world, with more than 36,000 described species (excluding Bruchinae) (Bouchard et al. 2009). However, recent estimates suggest that this number may be higher, ranging between 55,000 to 60,000 species (Jolivet 2015). This variety resulted from a diversification after the origin of their host plants, as well as from repeated radiations from preexisting diverse plant resources (Gómez-Zurita et al. 2007). Therefore, leaf beetles are almost entirely phytophagous, and their success in ecosystems is determined by their ability to occupy many different feeding niches (Jolivet 1988), and by their host specificity to almost all groups of plants (Riley et al. 2002). Most adults feed on living parts of plants, such as leaves, young stems, flowers, pollen, or fruits (White 1968, Wilcox 1972, Flowers 1996, Riley et al. 2002, Staines 2002, Jolivet and Verma 2008). The larvae are found on the surface of leaves or as leaf miners; others feed on roots, plant litter or submerged parts of plants (White 1968, Riley et al. 2002, Staines 2002, Jolivet and Verma 2008). Some larvae are myrmecophilous and feed on eggs and wastes of ants in their nests (Chamorro-Lacayo 2014). Therefore, leaf beetles are a key group in ecosystems as primary consumers, competing directly with other herbivores (González-Megías and Gómez 2003), and as important components in trophic webs (Basset and Samuelson 1996).

As phytophagous insects, the structure and composition of chrysomelid communities are determined largely by vegetation variables. These include, for example, the type and height of each forest stratum (floristic structure), percentage of vegetation or tree cover, diversity of plants, abundance of young foliage, and specific characteristics of the host plant (Bach 1981, Morrow et al. 1989, Řehounek 2002, Charles and Basset 2005, Baselga and Jiménez-Valverde 2007, Şen and Gök 2009, 2014). In addition, because of their food specificity, leaf beetles are also significantly impacted by modifications in various ecological gradients (Sánchez-Reyes et al. 2015, Sandoval-Becerra et al. 2017), which abiotic factors influence the ability to acquire available resources (Sandoval-Becerra et al. 2018). Therefore, any disturbance as a result of the loss of vegetation cover and land use change will have a direct effect on these insects (Wąsowska 2004).

After disturbance, secondary succession involves subsequent modifications of the vegetation following removal of vegetal cover, and it occurs through different routes, mechanisms, and processes (Pulsford et al. 2016). In turn, these modifications lead to further abiotic and microclimatic changes, which are related to seasonality (Lebrija-Trejos et al. 2011). Despite their importance, the consequences of fragmentation, disturbance, and secondary succession on chrysomelid communities have been quantified only in a few studies (Brown and Hyman 1986, Bach 1990), mainly in temperate wet forests (Linzmeier et al. 2006, Marinoni and Ganho 2006, Linzmeier and Ribeiro-Costa 2009, 2011) and tropical savannas (Pimenta and De-Marco 2015). In addition, in temperate oak forests of northeastern Mexico, the amount of time since last disturbance influences diversity, abundance and spatial distribution of Chrysomelidae (Sandoval-Becerra et al. 2018), as well as their microclimatic niche parameters (Sandoval-Becerra et al. 2017). On the other hand, few works have assessed consistently the effect of seasonality on successional changes of insect communities (Janzen 1976, Linzmeier and Ribeiro-Costa 2009), and some robust studies conducted during several years in areas with different level of conservation in South America, have shown a strong relation between leaf beetles and seasonal changes (Linzmeier and Ribeiro-Costa 2012, 2013). Thus, in order to standardize conservation strategies, it is necessary to evaluate whether the response patterns of leaf beetles to disturbance, secondary succession, and seasonality occur homogeneously in different habitats and ecosystems.

The extent of low thorn forest (LTF) vegetation in northeastern Mexico has been drastically reduced in the last 40 years (Sánchez-Reyes et al. 2017). This ecosystem harbors a high species richness of plants, with a large number of endemics (Rzedowski 2006), and, due to its geographical position, it shares characteristics (presence of deciduous or semi-deciduous species, climate regime) with other important subtropical communities, like the submontane scrub and Tamaulipan thorn scrub (García-Morales et al. 2014). Such floristic complexity presumably leads to a high species richness and diversity of leaf beetles, although this has not been evaluated since the faunistic studies of this family in Mexico are focused in other plant communities (Andrews and Gilbert 2005, Niño-Maldonado et al. 2005, Martínez-Sánchez et al. 2009, Furth 2013, Ordóñez-Reséndiz et al. 2015). In addition, a significant proportion of the current LTF cover in northeastern Mexico is composed of patches of conserved vegetation, together with large areas of secondary vegetation with varying lengths of succession time (Sánchez-Reyes et al. 2017). However, the influences of these disturbances and the time of secondary succession on the faunistic and ecological patterns of Chrysomelidae have never been quantified to date in this ecosystem.

The importance of evaluating changes in leaf beetle communities during secondary succession arises from their potential as indicator taxa. Chrysomelidae is cited as a useful family for monitoring local biodiversity (Farrell and Erwin 1988, Kalaichelvan and Verma 2005, Baselga and Novoa 2007, Aslan and Ayvaz 2009) and quality of the environment (Linzmeier et al. 2006), as well as assessing changes in natural areas (Staines and Staines 2001, Flowers and Hanson 2003). Since leaf beetles are sensitive to environmental modifications in the microhabitat (Sandoval-Becerra et al. 2017), the

changes in their community parameters and the presence of certain species could be useful to evaluate ecosystem integrity. However, only a few studies have quantitatively analyzed the indicator value of leaf beetles in the face of habitat changes after disturbance (Pimenta and De-Marco 2015, Sandoval-Becerra 2018). Therefore, the objectives of this study were to: 1) compose a faunistic list of Chrysomelidae in a low thorn forest fragment, 2) compare the species richness, abundance, and diversity in areas with different times of succession, 3) evaluate the seasonal effect in the successional stages, and 4) quantify the indicator value of chrysomelid species to secondary succession.

Methods

Study area

The study was conducted in a LTF fragment, located in the municipality of Victoria in the state of Tamaulipas, northeastern Mexico. In order to rule out the influence of topography on successional community patterns, a specific polygon of approximately 400 hectares was delimited on a plain area with little slope, at a homogeneous elevation between 320 and 350 m a.s.l. (23°51.75'N, 99°14'W and 23°51'N, 99°13.25'W). In addition, the area was located on the eastern foothills of the Sierra Madre Oriental, adjacent to the rural localities of Ejido (Ej.) Rancho Nuevo and Ej. Santa Ana (Figure 1).

Climate is classified as warm subhumid with summer rains, with an average annual temperature between 18 °C and 24.3 °C, and a total annual rainfall of 717.3 to 1058.8 mm (Almaguer-Sierra 2005). The highest volume of precipitation occurs between May and October, although occasional rains of less intensity may occur in other months. Due to this climatic regime, LTF vegetation in northeastern Mexico, particularly in the state of Tamaulipas, can be characterized as deciduous (INEGI, 2013) or semideciduous (Treviño-Carreón and Valiente-Banuet 2005). However, there are long drought periods without rain for several months; so, the vegetation could also be classified as a dry forest (Challenger and Soberón 2008), although not with as strongly marked seasonality as that observed in communities of the Mexican Pacific (Ceballos et al. 2010, Trejo 2010). Among the dominant plant species are *Celtis pallida* Torr., *Casimiroa greggi* (S. Watson) F. Chiang, *Ebenopsis ebano* (Berland.) Barneby & JW Grimes, *Havardia pallens* (Benth.) Britton & Rose, *Randia obcordata* S Watson, *Cordia boissieri* A DC, and *Croton cortesianus* Kunth. In addition, the LTF in the study area is mixed with communities of submontane scrub and Tamaulipan thorn scrub (Treviño-Carreón and Valiente-Banuet 2005, INEGI 2013, García-Morales et al. 2014). In this way, it constitutes a complex plant community of high diversity, with a notable number of endemic plants (García-Morales et al. 2014).

To the southwest, the study area approaches the Natural Protected Area Altas Cumbres (NPAAC, Figure 1), which constitutes a focal point for biodiversity in northeastern Mexico (Morrone and Márquez 2008, Secretaría de Gobierno 2015). However, the distribution of LTF in the areas surrounding the NPAAC, including the studied fragment, has been reduced significantly from 1973 to 2015 due to land use-cover

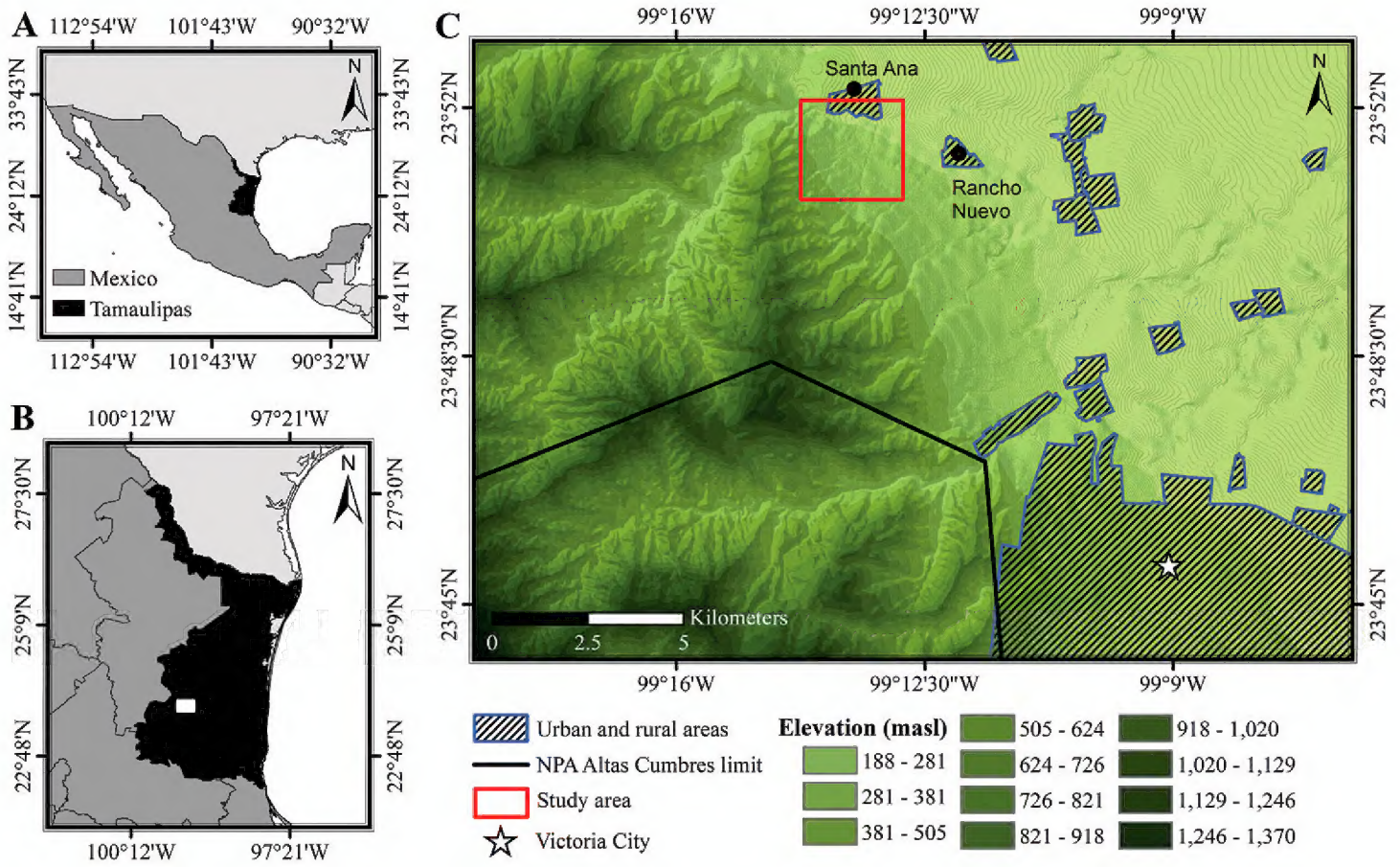

Figure 1. Location of the low thorn forest fragment in northeastern Mexico. **A** Tamaulipas, Mexico **B** location of the fragment within the State **C** detailed location of the LTF fragment in the foothills of the Sierra Madre Oriental, north of the Natural Protected Area Altas Cumbres.

change as a result of frequent fires and conversion to agriculture areas (Sánchez-Reyes et al. 2017), and is currently endangered (Secretaría de Gobierno 2015). Therefore, the study area constitutes a fragment of LTF composed of patches with differing degrees of conservation and times of secondary succession (Sánchez-Reyes et al. 2017).

Successional gradient delimitation

In the study of secondary succession, it is not always possible to measure the process of modification in a vegetal community over time, usually several years, in the same plot or site (Foster and Tilman 2000, Myster and Malahy 2008). An alternative to evaluate these changes is the use of chronosequences, where the study of succession takes place in space instead of time (Walker et al. 2010). Through this approach, it is assumed, among other factors, that selected sites have the same recovery history and that all succession stages have been developed under similar conditions (Denslow and Guzman 2000, Walker et al. 2010). However, these conditions are rarely considered when succession analysis is performed with chronosequences (Johnson and Miyanishi 2008). The use of geographic information systems and satellite images is an effective strategy to assess these assumptions when quantifying the recovery time on vegetation (Vieira et al. 2003, Arroyo-Mora et al. 2005); so, it can be a useful tool for establishing succession time and delimiting valid chronosequences (Sánchez-Reyes et al. 2017).

Table 1. Land use and cover categories in the study area.

Land cover/land use	Description	Reclassification
Conserved low thorn forest	Primary, conserved vegetation of low deciduous or semi-deciduous thorn forest.	Vegetation
Secondary vegetation of low thorn forest	Secondary arboreal vegetation of low thorn forest; predominance of arboreal species characteristic of submontane scrub and Tamaulipan thorn scrub.	Vegetation
Modified areas	Disturbance areas. Dense or low crop vegetation, active or abandoned agricultural areas, low secondary herbaceous vegetation, grassland cover at ground level.	Disturbance
Bare soil areas	Disturbance areas. Sparse or absent vegetation, dry rivers, rocks, bare soil, rural areas or buildings (human settlements).	Disturbance

Table 2. Transitional and persistence processes used to delimit succession categories in the study area. 1 = presence of vegetation (conserved and secondary low thorn forest); 0 = presence of disturbance (modified and bare soil areas).

Category / time of succession	Description	Landsat image					Field validation
		1973	1986	2000	2005	2013	2016, 2017
Conserved areas	Areas with vegetation in 1973 that remained unchanged until 2017	1	1	1	1	1	1
44 years	Areas with disturbance in 1973, but with vegetation in 1986, which persisted until 2017	0	1	1	1	1	1
31 years	Areas with disturbance in 1986, but with vegetation in 2000, which persisted until 2017	–	0	1	1	1	1
17 years	Areas with disturbance in 2000, but with vegetation in 2005, which persisted until 2017	–	–	0	1	1	1
12 years	Areas with disturbance in 2005, but with vegetation in 2017	–	–	–	0	1	1
4 years	Areas with disturbance in 2013, but with vegetation in 2017	–	–	–	–	0	1
Persistence of disturbance	Areas with disturbance in 1973, and remaining unchanged until 2017	0	0	0	0	0	0

We followed the chronosequence approach in this study. Delimitation of succession time of the LTF in the study area was carried out through the analysis of Landsat satellite images of the years 1973, 1986, 2000, 2005 and 2013 (Gutman et al. 2013), employing previously established methodology to calculate the approximate time of succession and define valid chronosequences (Sánchez-Reyes et al. 2017). Briefly, through this method, each of the five images was classified into four types of land use and cover (Table 1), using an unsupervised segmentation, together with the manual selection of training fields and the maximum likelihood algorithm. Afterwards, the four land use and cover categories were unified by means of an image reclassification into only two categories: vegetation and disturbance (Table 1). Finally, the reclassified images were subjected to a cross-tabulation analysis to delimit the time of succession, based on the date since the last disturbance and the transition or persistence of vegetation (LTF) from 1973 to 2013 (Table 2). Complementarily, the current presence of vegetation or disturbance was validated directly in the field during 2016–2017, as well as with recent Google Earth images. In this way, the final succession time in each area was delimited by the changes from 1973 to 2017 (Table 2). Procedures were conducted in the software IDRISI Selva 17.0.

Leaf beetles sampling

Sampling sites were selected according to the extent, location, and accessibility of the successional patches in the study area. Only four categories were selected for this study: 1) areas with four years of succession, 2) areas with 17 years of succession, 3) areas with 31 years of succession, and 4) conserved areas (Figure 2). In each of the four categories, a sample size of eight plots of 10 × 10 m was established; sample size was delimited through the analysis of preliminary data with the Clench model (Jiménez-Valverde and Hortal 2003). Sampling plots were located randomly using a previously established procedure (Sánchez-Reyes et al. 2016) using geographic information systems and specialized software (ArcView GIS, IDRISI Selva 17.0). With this method, it was possible to assess the geographical location of each plot before field sampling, in order to minimize the edge effect, as well as the closeness between plots, which guarantees the feasibility of sampling and the independence of the samples.

Leaf beetles were sampled using an entomological sweep net (60 centimeters long and 40 centimeters in diameter). Each sample consisted of 200 sweeps on all the shrub and herbaceous vegetation in each plot, from soil level up to a maximum height of 2 m, between 10:00 and 14:00 hrs. All contents of the net after 200 sweeps were deposited

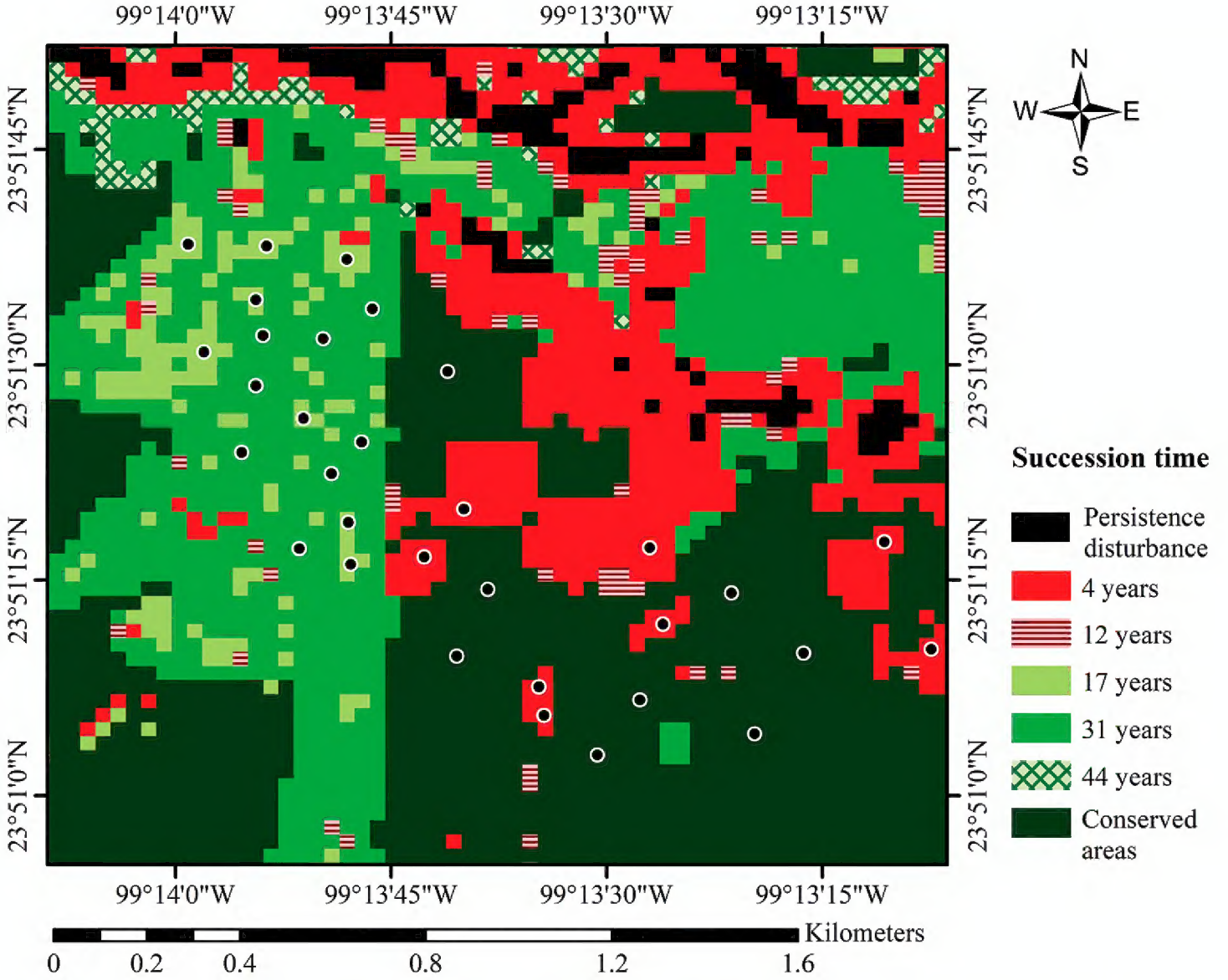

Figure 2. Successional gradient of low thorn forest in northeastern Mexico, and location of the sampling plots.

in a plastic bag, adding 70 % ethyl alcohol, as well as a label with the corresponding data. Each plot of each successional category was sampled once a month, from May 2016 to April 2017, for a total of 384 samples (8 plots x 4 categories x 12 months).

The processing of samples and preparation of specimens were conducted in the laboratory according to previously established methods (Sánchez-Reyes et al. 2014). Taxonomic identification was made using specialized literature (Wilcox 1965, Wilcox 1972, Scherer 1983, White 1993, Flowers 1996, Riley et al. 2002, Staines 2002) and by comparison with specimens in the collection of the Facultad de Ingeniería y Ciencias, Universidad Autónoma de Tamaulipas (FIC-UAT), and identified taxa were organized following the arrangement proposed by Riley et al. (2003) and Bouchard et al. (2011). Specimens that could not be identified to species level were differentiated as morphospecies, based on characteristics of internal genitalia. In this way, the term "species" in this study includes both specimens determined at a specific level and morphospecies. Specimens were deposited in collections of the Instituto Tecnológico de Ciudad Victoria (ITCV) and the FIC-UAT, as well as in the personal collection of the first author (IC-UJSR).

Data analysis

The observed species richness was measured as the total number of species in the LTF fragment, as well as at each successional category. Significant differences in the number of species among categories were determined by the diversity permutation test implemented in PAST 3.07 (Hammer et al. 2001). Estimated species richness was calculated for the entire study area and for each category, using the Chao 1, Chao 2, Jackknife 1, Jackknife 2, ACE and ICE nonparametric indices. Inclusion of these indices is recommended in biodiversity studies to evaluate the estimated range of species in the faunistic inventory (Hortal et al. 2006); calculations were made in EstimateS 8.2 (Colwell 2013), using 100 randomizations without replacement. We also calculated the estimated species richness through the Clench model, as well as the slope value, in order to determine the quality of inventories, where values close to or less than 0.1 are considered characteristic of reliable inventories (Jiménez-Valverde and Hortal 2003). The Clench model was performed in STATISTICA 8.0 (StatSoft Inc. 2007), following the parameters indicated by Jiménez-Valverde and Hortal (2003). Completeness of the total inventory and of each category was obtained as the proportion of observed richness with respect only to the estimated value of the Chao 1 index, since it takes into account the abundance of species and acts as a lower bound for species richness (Chao and Chiu 2016), and was expressed as percentage.

Overall differences in abundance of leaf beetle communities in the successional gradient were calculated with the Kruskal-Wallis test, after discarding a normal distribution. In addition, significant differences in abundance between categories were obtained through pairwise comparisons, using the Mann-Whitney test. Diversity was considered as a proportional value between species richness and abundance values,

and was quantified by Simpson's dominance index and the Shannon entropy index (Magurran 2004); these were calculated for the entire study area and for each successional category. Pairwise comparisons of diversity values between categories were carried out using the diversity permutation test. Changes in species composition between successional categories were evaluated by comparing faunistic similarity, using the Bray-Curtis index (Magurran 2004). All analyzes were performed in PAST 3.07.

Seasonal effect was measured separately, by comparing observed and estimated species richness, abundance, and diversity in each category during the rainy (May to October 2016) and dry seasons (November 2016 to April 2017); differences in abiotic conditions between both seasons were confirmed in a previous study (Sánchez-Reyes et al. in press). The aforementioned indices and statistical tests were used for such comparisons: nonparametric estimation of species richness, Kruskal-Wallis and Mann-Whitney tests for differences in abundance, diversity permutation tests for observed species richness, and Simpson and Shannon indices, which were conducted in PAST 3.07. An agglomerative Cluster analysis was performed in order to include the seasonal effect in faunistic composition, with the objective of grouping categories and seasons according to their similarity in species composition. For this, a dissimilarity matrix based on Bray-Curtis distance and Ward's amalgamation algorithm was used. Cluster analysis was performed in STATISTICA 8.0.

The indicator value of chrysomelid species was quantified by the Indicator Value Index, or IndVal (Dufrêne and Legendre 1997). The index is based on the degree of specificity (exclusivity of the species to a particular site based on its abundance) and the degree of fidelity (frequency of occurrence within the same habitat) (Tejeda-Cruz et al. 2008), expressed in a percentage value. The analysis was carried out using the *labsdv* package in platform R version 3.2.2, using 1000 random permutations to define the significance level. Indicator species with an index equal to or greater than 70 % were categorized as "characteristic" species, while species with a value less than 70 % but equal to or greater than 30 % were considered "detector" species.

Results

Successional variation of leaf beetle communities

In total, 6978 specimens of leaf beetles were collected distributed in six subfamilies, 57 genera, and 85 species (Appendix 1). The greatest abundance and species richness were observed in the subfamily Galerucinae (6416 specimens and 40 species respectively). Total values of estimated richness in the low thorn forest fragment suggested a reliable inventory (slope = 0.029), with a total completeness of 82.52 %. The dominance was 0.284, while the Shannon index was 2.009 (Table 3).

The analysis of successional categories revealed that the species richness was significantly higher in the areas of four years of succession. The conserved areas also demonstrated a high number of species, although the value was similar to that observed

Table 3. Succession parameters of leaf beetle communities in a low thorn forest in northeastern Mexico.

Ecological parameter	Low thorn forest total	Succession time			
		4 years	17 years	31 years	Conserved areas
Observed richness*	85	58 a	36 b	31 b	45 ab
Chao 1	103	70.07	66.23	33.57	52.55
Chao 2	97.86	72.07	53.81	34.96	56.95
Jackknife 1	103.95	73.83	47.88	38.92	57.86
Jackknife 2	108.96	80.78	55.75	39	63.81
ICE	101.34	71.4	44.43	37.63	58.64
ACE	99.91	68.05	44.52	34.9	52.43
Clench model	95.53	68.40	46.32	40.27	55.16
Slope	0.029	0.103	0.087	0.075	0.093
Completeness (%)	82.52	82.77	54.35	92.34	85.63
Abundance*	6978	2725 a	1753 a	1674 ab	826 b
Dominance (Simpson index)*	0.2841	0.2174 a	0.6543 b	0.781 c	0.1469 d
Diversity (Shannon index)*	2.009	2.084 a	0.9797 b	0.6796 c	2.521 d

*Different letters between columns are significantly different from each other.

Table 4. Faunistic similarity of Chrysomelidae between successional categories of a low thorn forest in northeastern Mexico. Upper diagonal, values of the Bray-Curtis index. Lower diagonal, values expressed in percentage.

	4 years	17 years	31 years	Conserved areas
4 years	1	0.3135	0.2629	0.2225
17 years	31.35 %	1	0.9456	0.2300
31 years	26.29 %	94.56 %	1	0.2265
Conserved areas	22.25 %	23 %	22.65 %	1

in the intermediate categories (17 and 31 years of succession). In all categories, the inventories were reliable according to the Clench slope values, and the observed species richness values were close to the estimated values; areas of 4 and 31 years of succession, as well as conserved areas, had a completeness value above 70 %. However, a low value of completeness (54.35 %) was obtained only in the areas of 17 years of succession (Table 3). The abundance decreased significantly with the increase in time of succession ($H = 12.56$, $p = 0.005$). Thus, early succession sites had the highest number of specimens when compared to the conserved areas. The values of diversity were significantly different among all the categories ($p < 0.05$). Highest dominance and lowest diversity were obtained in the intermediate succession areas (17 and 31 years); in contrast, the conserved areas recorded the highest diversity value (Table 3).

With respect to the Bray-Curtis index, a very high similarity was observed in the faunistic composition between the intermediate (17 and 31 years) successional areas (94.56 %). Remaining comparisons were below 50 % similarity (Table 4).

Effect of seasonality on the successional changes of Chrysomelidae

Seasonal effect was absent in the observed species richness, since there were no significant differences ($p > 0.05$) between the rainy and dry seasons in any of the four categories (Figure 3). The estimated richness analysis revealed that both inventory reliability and completeness were higher in the dry season than in the rainy season, in all categories (Table 5). On the other hand, in all cases the completeness was higher than 70 %; however, in the 17-year category, the estimated richness reached very high proportions during the rainy season, with a total completeness of 35.54 % (Table 5).

Differences in abundance between the rainy and dry season were significant in each category ($p < 0.05$), except for the conserved areas where the number of specimens was similar in both seasons ($p = 0.0904$). In addition, during the rainy season, the abundances observed in the areas of 4, 17, and 31 years were similar, but significantly different from the conserved areas; contrarily, during the dry season there were no differences in abundance between categories (Figure 3). Regarding diversity, the seasonal effect was not observed in the areas of 4 years of succession, since there were no differences in either the Simpson or Shannon indices between seasons. In the case of the intermediate areas (17 and 31 years of succession), lower dominance and higher diversity occurred during the dry season. Conversely, the minimum dominance and maximum diversity values in the study area were obtained in the conserved areas during the rainy season (Figure 3).

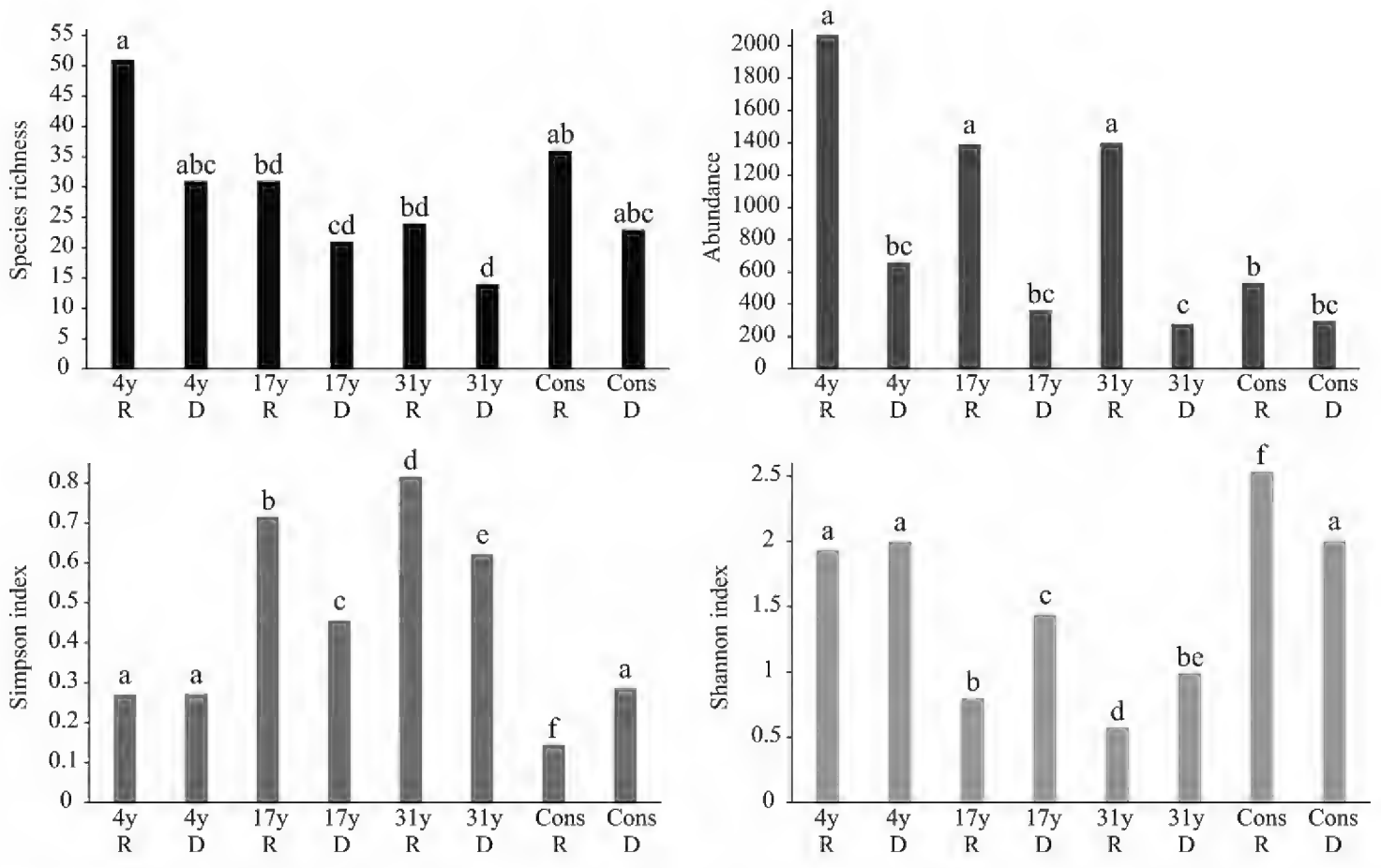

Figure 3. Seasonal variation of community parameters of Chrysomelidae in a successional gradient of low thorn forest in northeastern Mexico. Different letters between bars indicate significant differences.

Table 5. Influence of seasonality on the estimated species richness and inventory completeness of successional categories in a low thorn forest in northeastern Mexico.

	4 years		17 years		31 years		Conserved	
Estimator index	**Rainy**	**Dry**	**Rainy**	**Dry**	**Rainy**	**Dry**	**Rainy**	**Dry**
Chao 1	70.59	31.64	87.21	21.07	27.12	14.1	42.39	23.9
Chao 2	71.21	31.37	66.37	21.05	32	14.06	52.32	23.63
Jack 1	67.65	33.94	47.65	21.98	30.85	14.98	45.79	25.94
Jack 2	77.37	25.56	60.19	13.56	34.75	8.43	52.56	22.25
ICE	68.37	32.09	66.59	21.36	29.21	14.4	44.56	24.6
ACE	63.47	32.35	57.91	21.36	27.45	14.47	42.27	24.82
Clench model	63.12	38.40	47.94	27.51	30.67	18.80	43.22	28.69
Slope	0.222	0.121	0.233	0.096	0.111	0.071	0.136	0.091
Completeness (%)	72.24	97.97	35.54	99.66	88.49	99.29	84.92	96.23

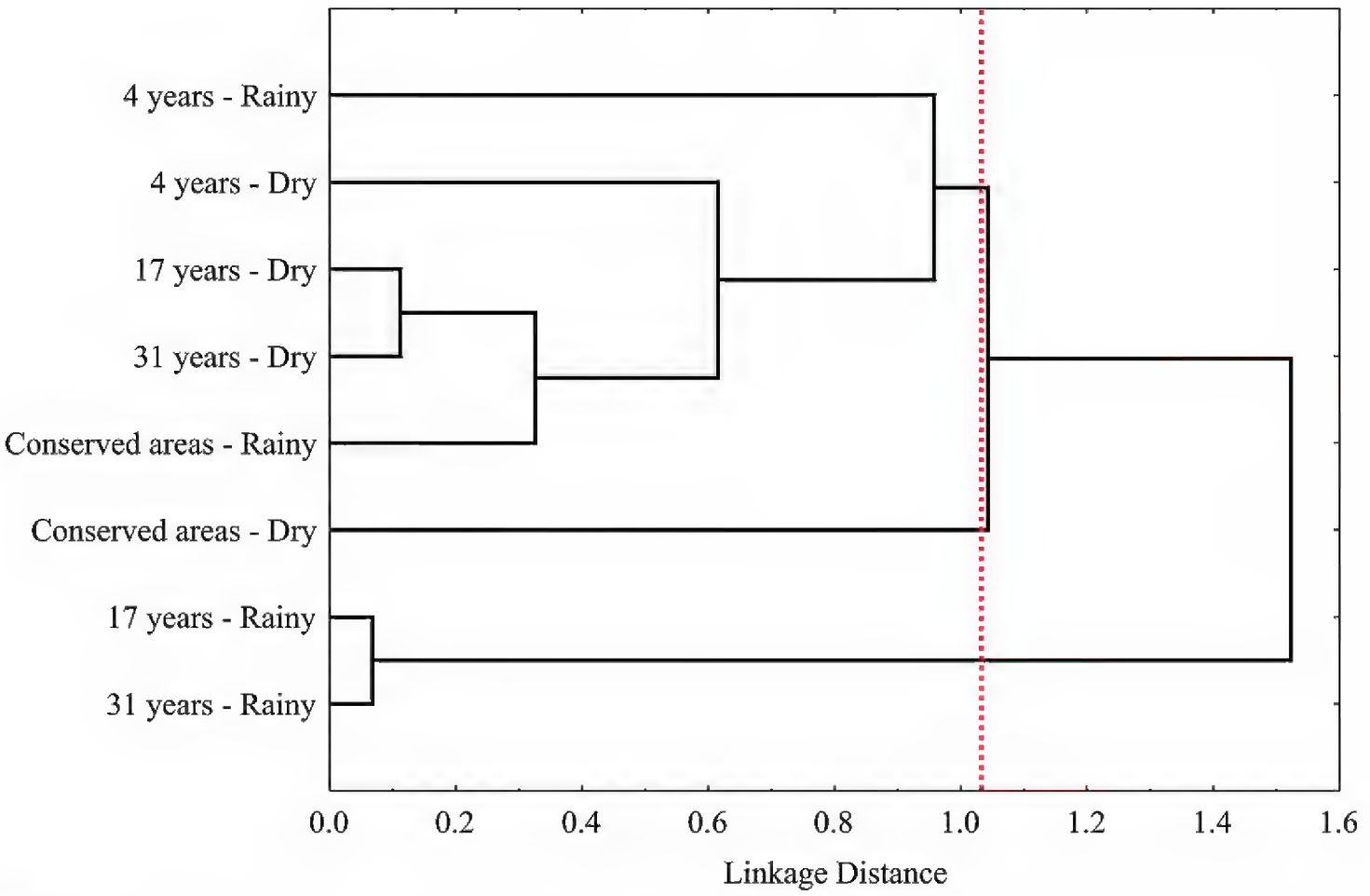

Figure 4. Cluster analysis of leaf beetle composition between succession and seasonal categories (rainy and dry) in a low thorn forest in northeastern Mexico. The dotted line indicates the delimitation of the groups.

The analysis of similarity in species composition between successional categories, considering the seasonal effect, suggested the presence of three faunistic groups. The first group consisted of the areas of 17 and 31 years of succession during the rainy season. Conserved areas during the dry season represented another group. The category of four years of succession, intermediate areas during the dry season, and conserved areas in the rainy season formed a third group with higher heterogeneity (Figure 4).

Indicator value of leaf beetles in the successional gradient

Of the 85 total species found in the LTF, only 24 had a significant indicator value ($p < 0.05$, Table 6, Figures 5, 6). The highest proportion involved detector species, with an IndVal between 30 and 70 % (17 species). The remaining seven were characteristic species, with values higher than 70 % (Table 6). Four species were considered as characteristic of areas with four years of succession, of which *Brachycoryna pumila* Guérin-Méneville, 1844 and *Chaetocnema* sp. 1 had the highest indicator values; the other six species were detectors of this category. *Cyclotrypema furcata* (Olivier, 1808) and *Heterispa vinula* (Erichson, 1847) were detector species of areas with 17 years of succession, while *Centralaphthona diversa* (Baly, 1877), *Dysphenges* sp. 1 and *Sumitrosis inaequalis* (Weber, 1801) were detectors of 31 years of succession. In the conserved areas, six species were detectors; only *Acrocyum dorsalis* Jacoby, 1885, *Margaridisa* sp. 1 and *Parchicola* sp. 1 were characteristic indicators, the latter being the one with the highest specificity.

Table 6. Leaf beetle species with a significant indicator value in a successional gradient of low thorn forest in northeastern Mexico. Indicator values in succession categories are expressed in percentage. Key: C = characteristic; D = Detector, *p* = probability.

Species	Succession time				*p*	Indicator category
	4 years	17 years	31 years	Conserved areas		
Acallepitrix sp. 1	0.00	7.89	0.66	47.37	0.0048	D
Acrocyum dorsalis	0.00	0.00	0.00	75.00	0.0003	C
Alagoasa jacobiana	4.46	2.38	5.36	56.25	0.0017	D
Asphaera sp. 1	34.09	1.14	0.00	0.00	0.0433	D
Babia tetraspilota texana	53.85	7.21	11.54	0.48	0.0021	D
Brachycoryna pumila	88.73	2.82	0.00	0.00	0.0001	C
Centralaphthona diversa	11.08	40.83	42.74	5.35	0.0241	D
Chaetocnema sp. 1	93.47	5.55	0.00	0.02	0.0001	C
Colaspis townsendi	53.35	0.30	0.00	3.05	0.0072	D
Cryptocephalus trizonatus	37.50	0.00	0.00	0.00	0.0492	D
Cyclotrypema furcata	30.65	55.91	0.81	0.00	0.0047	D
Dysphenges sp. 1	21.88	14.51	42.19	0.45	0.0282	D
Epitrix sp. 1	90.87	0.15	0.02	5.24	0.0001	C
Epitrix sp. 2	19.44	4.86	0.52	63.89	0.0001	D
Epitrix sp. 3	75.38	0.34	0.10	3.89	0.0003	C
Epitrix sp. 4	7.34	0.27	0.00	58.70	0.0036	D
Epitrix sp. 5	1.97	7.89	0.00	39.47	0.0327	D
Helocassis clavata	5.07	2.70	0.68	61.49	0.0014	D
Heterispa vinula	7.50	45.21	18.33	0.97	0.0351	D
Margaridisa sp. 1	12.74	0.12	1.14	72.96	0.0002	C
Parchicola sp. 1	1.32	0.00	0.00	78.29	0.0001	C
Parchicola sp. 2	37.50	0.00	0.00	0.00	0.0483	D
Plagiodera thymaloides	42.86	0.45	19.64	0.00	0.0257	D
Sumitrosis inaequalis	0.83	5.00	36.67	0.00	0.0353	D

Figure 5. Chrysomelidae species with significant indicator value of successional time in a low thorn forest fragment in northeastern Mexico. **A** *Acallepitrix* sp. 1 **B** *Epitrix* sp. 5 **C** *Acrocyum dorsalis* Jacoby, 1885 **D** *Alagoasa jacobiana* (Horn, 1889) **E** *Asphaera* sp. 1 **F** *Babia tetraspilota texana* Schaeffer, 1933 **G** *Brachycoryna pumila* Guérin-Méneville, 1844 **H** *Centralaphthona diversa* (Baly, 1877) **I** *Chaetocnema* sp. 1 **J** *Colaspis townsendi* Bowditch, 1921 **K** *Cryptocephalus trizonatus* Suffrian, 1858 **L** *Cyclotrypema furcata* (Olivier, 1808). Scale bar: 1 mm.

Figure 6. Chrysomelidae species with significant indicator value of successional time in a low thorn forest fragment in northeastern Mexico. **A** *Dysphenges* sp. 1 **B** *Epitrix* sp. 1 **C** *Epitrix* sp. 2 **D** *Epitrix* sp. 3 **E** *Epitrix* sp. 4 **F** *Helocassis clavata* (Fabricius, 1798) **G** *Heterispa vinula* (Erichson, 1847) **H** *Margaridisa* sp. 1 **I** *Parchicola* sp. 1 **J** *Parchicola* sp. 2 **K** *Plagiodera thymaloides* Stål, 1860 **L** *Sumitrosis inaequalis* (Weber, 1801). Scale bar: 1 mm.

Discussion

The present study constitutes the first faunistic contribution of Chrysomelidae in the low thorn forest vegetation. The observed species richness and completeness values suggest that the fauna of leaf beetles in the LTF is close or superior to other types of low tropical forest (Sánchez-Reyes et al. 2014, Lucio-García 2018). In general terms, the values represent 34 % of the observed chrysomelid richness in Tamaulipas (Niño-Maldonado et al. 2014), as well as 3.19 % of the country-wide values (Niño-Maldonado and Sánchez-Reyes 2017). In addition, the abundance values were higher than for other studies carried out in the region, including those conducted in larger geographical areas also during an annual period (Niño-Maldonado et al. 2005, Sánchez-Reyes et al. 2014, 2016). One of the factors that can give rise to such results is the complexity of the plant structure in the study area, which consists of tropical vegetation elements in conjunction with species from semi-arid or subtropical areas, such as Tamaulipan thorn scrub or submontane scrub (Treviño-Carreón and Valiente-Banuet 2005, García-Morales et al. 2014). This floristic complexity was mirrored in the presence of an equally complex chrysomelid fauna. In addition, the proximity to the NPA Altas Cumbres (Secretaría de Gobierno 2015) and the adjacent location of one of the panbiogeographic nodes of Mexico (Morrone and Márquez 2008) should undoubtedly be related to the species composition observed.

However, the environmental heterogeneity in the LTF, resulting from disturbance and secondary succession, is perhaps the most important factor leading to the observed patterns. Previous studies had been carried out mainly in natural protected areas, where ecosystems have a high degree of conservation and low occurrence of fragmentation (Niño-Maldonado et al. 2005, Sánchez-Reyes et al. 2014, 2016). Contrastingly, LTF in northeastern Mexico, particularly in the eastern boundaries of the NPA Altas Cumbres, constitutes a highly heterogeneous habitat, which has been subject to strong fragmentation and presently is composed of patches with different succession times (Sánchez-Reyes et al. 2017). Environmental heterogeneity is one determining factor in the structure of communities, and, although it can be variable, its increase is positively related to the species richness (Tamme et al. 2010, Stein et al. 2014, Yang et al. 2015). Such an effect has been observed in other studies of Chrysomelidae; for example, in temperate forests of northeastern Mexico, a high diversity is associated with a heterogeneous mosaic of vegetation with different times since last disturbance (Sandoval-Becerra et al. 2018). In that sense, the influence of heterogeneity was made evident in this study through the detailed comparisons of species richness, abundance, and diversity between areas with different times of succession.

Responses of communities to disturbance are diverse (Winter et al. 2015). Overall, in the LTF the greatest number of species occurred in the category of 4 years of succession. Early successional areas (those without dense tree cover or with open canopy) can promote diversity due to their high structural and spatial complexity (Swanson et al. 2011). On the other hand, the estimators were very close to the observed richness for each successional category, indicating that faunistic inventory was nearly complete,

and thus that the calculated parameters are reliable. Several studies in disturbance-succession gradients found that the greatest number of insects occurred in advanced stages of recovery, or in mature, conserved areas (Barberena-Arias and Aide 2003, Jeffries et al. 2006, Villa-Galaviz et al. 2012, Perry et al. 2016). However, this depends on the ecological characteristics of the taxa analyzed, since disturbance can contribute to the increase in diversity (Steffan-Dewenter and Tscharntke 2001, Stephen and Sánchez 2014, Winter et al. 2015, Yuan et al. 2016, O'Brien et al. 2017). In the case of leaf beetles, it has been observed that species richness augments in modified areas (Heusi-Silveira et al. 2012), as was observed in this study. This is because, in recently disturbed or early succession areas, the density of herbaceous and shrub plants is usually higher. This favors the presence of a greater number of phytophagous insects in these areas, given their close association with successional changes of vegetation (Fernandes et al. 2010, O'Brien et al. 2017). In addition, in the area of this study, the early succession stages of LTF are also dominated by species from other plant communities, such as submontane scrub or Tamaulipan thorn scrub (Canizales-Velázquez et al. 2009). Therefore, early succession areas constitute habitats of a complex floristic structure, which triggers a higher environmental heterogeneity and thus explains the high number of chrysomelid species. With respect to abundance, the obtained results agree with trends observed in other studies, since the number of specimens decreased linearly from early succession to the most conserved areas (Heusi-Silveira et al. 2012, O'Brien et al. 2017). Similarly, this is attributed to a higher density of herbaceous and shrub plants in recently disturbed areas (Guariguata and Ostertag 2001, Pickett et al. 2008, Swanson et al. 2011). Besides, this decline in abundance was related to a drop in dominance values in conserved areas, in a way that this category registered the highest diversity, that is, the highest effective number of species considering an equitable community (Jost 2006). Over the course of succession, increase in stability of communities occurs, while fluctuations in availability of resources for species decrease (Anderson 2007). This homogeneity in environmental conditions allows for an even distribution in the relationship between species richness and abundance, thus increasing diversity (Magurran 2004).

Seasonality had a very important influence on the successional patterns. However, differences in species richness were non-existent between seasons. Thus, the number of leaf beetle species was similar throughout the year in each successional category. On the other hand, the number of specimens was significantly higher during the rainy season in all successional categories (4, 17, and 31 years); contrarily, no differences were observed in conserved areas. This is attributed to the vegetation characteristics in successional areas. An open structure of the canopy allows for a greater light input, which during the rainy season favors a high density of annual herbaceous and shrub species (Guariguata and Ostertag 2001, Pickett et al. 2008, Swanson et al. 2011), which constitute a very abundant food resource, but only during one season. Over the course of succession, dominance of shrubs and other perennial herbaceous plants increases (Swanson et al. 2011); indeed, the understory in conserved areas of LTF is dominated mostly by perennial or semiperennial species (Treviño-Carreón and Valiente-Banuet 2005, García-Morales et al. 2014), and these satisfy nourishing requirements of leaf

beetles even during the dry season. Such an effect of transition from annual to perennials plants during succession has also been observed in other groups of insects (Steffan-Dewenter and Tscharntke 2001).

With respect to diversity, the intermediate categories (17 and 31 years of succession) showed significantly higher values in the dry season, while in the conserved areas they were higher during the rainy season. Intermediate areas of LTF are spatially and floristically heterogeneous; thus, the existence of annual species from other scrub communities must be responsible for the drastic reduction of understory vegetation in the dry season; consequently, this causes the decrease in abundance, reducing dominance and increasing diversity. Oppositely, the environmental conditions during the rainy season in conserved areas seem to be supporting a greater availability of resources, in such a way that leaf beetle species are uniformly dispersed; this can be attributed to the higher specialization of species in mature or conserved areas (Pellissier 2015). In contrast, the absence of differences in seasonal diversity at early succession areas can be attributed to generalist species, which are dominant in highly heterogeneous areas (Büchi and Vuilleumier 2014). Consequently, dominance and diversity remain constant throughout the year, regardless of available resources in each season, since generalists feed on multiple plant species and tolerate a wide range of microclimatic conditions (Sandoval-Becerra et al. 2018). An example of such species is *Brachycoryna pumila*, because its abundance was higher in areas of four years of succession in both seasons, thus suggesting a wide abiotic tolerance; also, *B. pumila* is associated with several species of plants in different genera, such as *Abutilon*, *Malvastrum*, or *Sida*, among others (Staines 1986). However, biological and ecological information is lacking for most of the leaf beetle species in the region; therefore, future assessments on niche requirements of leaf beetles need to be conducted.

In addition to the consequences to abundance and diversity, disturbance and successional changes also influence species composition (Perry et al. 2016). For example, it has been observed that dry season results in greater faunistic similarity between different sites, despite having different degrees of conservation (Janzen 1976). Such an influence was evident in this work, since, according to the Cluster analysis, the areas of 4, 17, and 31 years had the same species composition during the dry season. Besides, the conserved areas had a totally different composition with respect to the other successional stages, which agrees with patterns observed in several other insect taxa (Barberena-Arias and Aide 2003, Perry et al. 2016). In this regard, early succession areas and high heterogeneity due to disturbance may indeed increase the number of species, as was discussed above; however, the similarity of faunistic composition between such areas and conserved sites is very low. Thus, it is necessary to point out the importance of the conserved areas for Chrysomelidae distribution in the low thorn forest vegetation, as their communities are unique to these types of habitats when compared with disturbed areas.

An important theory that aims to explain the relationship between disturbance and diversity is the intermediate disturbance hypothesis (IDH, Connell 1978, Willig and Presley 2018). It postulates that with the increase of the disturbance an imbalance is created in the environmental conditions, and that this reduces the probability of exclusion among coexisting species (Connell 1978, Huston 2014). Thus, intermediate areas

represent a convergence of both ends of the gradient, promoting greater heterogeneity in conditions that allows an increase in the resource availability, as well as in the richness and diversity of species (Shea et al. 2004, Bongers et al. 2009, Roxburgh et al. 2004, Winter et al. 2015). Also, intermediate areas may increase herbivory patterns (Chapin et al. 2011). The influence of IDH has been proven previously with Chrysomelidae in other types of vegetation (Linzmeier et al. 2006, Linzmeier and Ribeiro-Costa 2009, Sandoval-Becerra et al. 2018). Observed results in the LTF were contrary, since as explained above, the intermediate areas of 17 and 31 years of succession had very low values of richness and diversity. However, richness estimators can determine the validity of the IDH in the study area, because the category of 17 years of succession could reach above 87 species during the rainy season, while the completeness was higher in the other categories and seasons. Such an estimated value was close to the total observed richness for the entire LTF fragment, confirming that areas of 17 years are a heterogeneous environment with characteristics of both early and late successional stages, creating niches for numerous species (Sandoval-Becerra et al. 2018). It is possible that the randomized design of the study caused that location of most of the intermediate sampling plots fell in areas with low density of herbaceous and shrub vegetation, while only a few plots had contrasting conditions. Such differences would be enhanced due to a higher environmental heterogeneity in the rainy season. In addition, the convergence of species from early and late succession areas was supported by the higher faunistic similarity observed between the categories of 17 and 31 years of succession, even when including a seasonal effect. Therefore, it is fairly possible that community patterns of Chrysomelidae in the LTF are consistent with IDH, although future studies with a higher number of samples are necessary to corroborate this presumption.

Overall, the seasonal effect on leaf beetle communities has been previously assessed in natural gradients (Bouzan et al. 2015, Sánchez-Reyes et al. 2014, 2016). However, the interaction between seasonality and secondary succession, as investigated here, has been poorly quantified (Janzen 1976, Linzmeier and Ribeiro-Costa 2009). Analysis of these patterns is important to determine the magnitude of changes in insect communities after disturbance, so that conservation strategies can be applied successfully. Besides, the understanding of seasonal influence on successional trajectories is critical not only for leaf beetles, but also for other biological groups, since incoming environmental modifications due to climate change surely will affect the mechanisms in which communities response to disturbance, and will therefore affect their resilience aptitude. Hence, more studies are sorely needed in order to clarify these associations, since the responses to succession and disturbance are influenced by microenvironmental changes, and these responses differ depending on the species (Sandoval-Becerra et al. 2017).

Regarding the indicator potential of Chrysomelidae, other studies have suggested that the higher proportion and abundance of leaf beetles are characteristics of early succession or recently disturbed areas (Pimenta and De-Marco 2015), which was corroborated in this study. However, it is evident that the observed community patterns (such as abundance) are driven by the specific response of each species, since leaf beetles can tolerate different microclimatic and microhabitat conditions after disturbance (Sand-

oval-Becerra et al. 2017). Therefore, these characteristics may allow species within this family to be used as indicators. The potential of leaf beetles for environmental monitoring has been suggested by other authors (Nummelin and Borowiec 1992, Flowers and Hanson 2003, Linzmeier et al. 2006). Similarly, the usefulness of chrysomelid diversity as an indicator of plant species richness has been recognized (Kalaichelvan and Verma 2005, Baselga and Novoa 2007). However, only a few exceptional studies have presented quantifiable indicator values (Pimenta and De-Marco 2015).

The indicator value index (IndVal) allows for statistical evaluation of the degree of association between species and their environment (Dufrêne and Legendre 1997, De-Cáceres et al. 2012). Species with a significant IndVal can be separated into characteristic and detector species, according to their specificity towards a particular habitat condition. The characteristic indicator species are those with high specificity and fidelity to a given habitat, and therefore a high percentage of indicator value (Dufrêne and Legendre 1997, McGeoch et al. 2002, Tejeda-Cruz et al. 2008). These may be important from an ecological perspective, but not very useful for disturbance quantification, since their presence is exclusive of certain habitats and thus the destruction or modification of such areas would drive local extinction (Hodkinson and Jackson 2005). In contrast, indicator species with moderate levels of specificity (i.e., detector species) have differing degrees of preference for the various ecological states (Dufrêne and Legendre 1997, McGeoch et al. 2002, Tejeda-Cruz et al. 2008). Such detector species are ideal for monitoring, because their wide niche breadth and their changes in abundance during disturbance ensure that they can be dispersed along a disturbance gradient (McGeoch et al. 2002, Hodkinson and Jackson 2005). Accordingly, we consider that indicator species in this study, such as *Centralaphthona diversa*, *Cyclotrypema furcata* and *Heterispa vinula*, are potentially suitable as indicators of succession time and for environmental monitoring in other areas with similar vegetation; in addition, species like *Acrocyum dorsalis* could be useful to detect conserved areas of LTF (Figure 7). These species are easily identifiable (even in the field), are abundant (so their proportion in different degrees of disturbance can be statistically quantified), and are widely distributed in the region (Niño-Maldonado et al. 2014, Sánchez-Reyes et al. 2016). Therefore, they fulfill the expected characteristics for a good indicator taxon (Carignan and Villard 2002, Ribera and Foster 1997). Besides, their response as significant indicator species is consistent with other ecological gradients, such as microclimate or elevation (Sánchez-Reyes et al. 2016, 2017). However, their presence as an indicator in this study does not guarantee that their response to succession time will be homogeneous in other areas; such responses must be consistent and repeatable in different sites and time scales in order to consider a species as a reliable indicator (McGeoch et al. 2002, Hodkinson and Jackson 2005). Currently, we suggest the inclusion and use of these (and maybe the other species that were found) for the monitoring of secondary vegetation and quantification of succession time in LTF in northeastern Mexico. Further evidence of their usefulness as indicator species will contribute to the implementation of new and better conservation strategies, and to an efficient delimitation of natural protected areas which take into account the importance of secondary vegetation for species distribution.

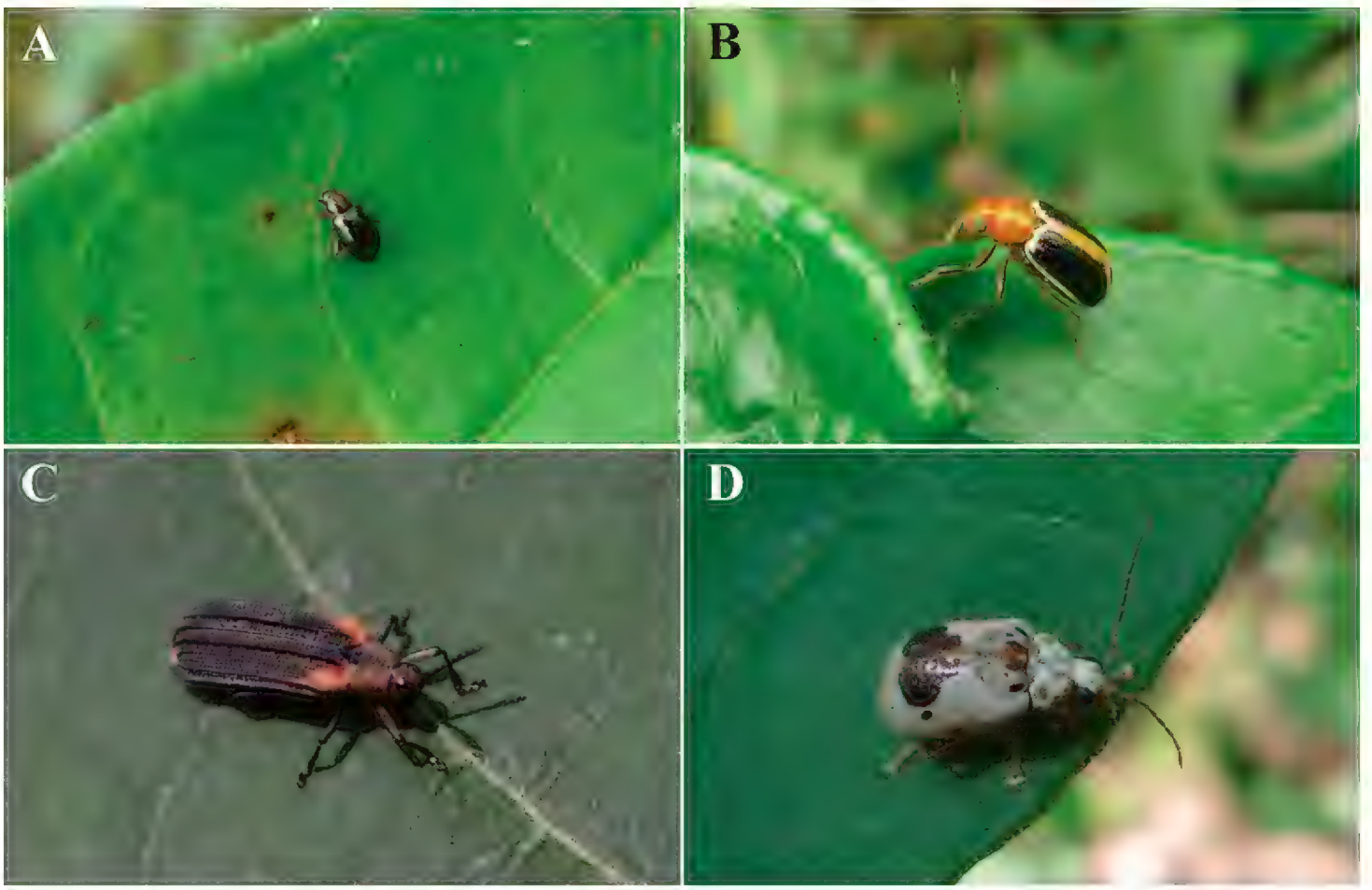

Figure 7. Suggested species of Chrysomelidae for evaluating successional time and environmental monitoring of low thorn forest in northeastern Mexico. **A** *Centralaphthona diversa* (Baly, 1877) **B** *Cyclotrypema furcata* (Olivier, 1808) **C** *Heterispa vinula* (Erichson, 1847) **D** *Acrocyum dorsalis* Jacoby, 1885.

Conclusions

The study of effects of disturbance and secondary succession on species and communities is a key issue in ecology and conservation. In that sense, faunistic patterns of leaf beetles and their association to secondary succession are evaluated for first time in low thorn forest vegetation in northeastern Mexico. A highly fragmented landscape in early and intermediate successional stages, as well as the convergence of other vegetation communities, could be related to the high number of species found, due to a complex environmental heterogeneity. Overall, observed changes in communities were similar to those observed in other studies with leaf beetles in disturbance gradients. However, the inclusion of a seasonal effect results in some differences, depending on the evaluated parameter. Seasonal changes trigger differences in abundance, diversity, and species composition, but not in species richness, in each category and between categories. Major influence of seasonality occurred at intermediate successional categories, which could be due to the influence of intermediate disturbance hypothesis. Therefore, we point out the importance of evidence here obtained, since the influence of seasonal changes on successional trajectories is important for every biological taxon. Thus, accelerating climate change would exert modifications in the way communities are structured during secondary succession after disturbance, which is of major importance for species and ecosystem restoration. On the other hand, we propose that the use of

several species of leaf beetles for monitoring secondary vegetation and quantifying the succession time of low thorn forest is feasible, at least in northeastern Mexico. However, further studies are necessary to assess the potential of these and other species of leaf beetles to be indicators.

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References

Almaguer-Sierra P (2005) Fisiografía del Estado de Tamaulipas. In: Barrientos-Lozano L, Correa-Sandoval A, Horta-Vega JV, García-Jiménez J (Eds) Biodiversidad Tamaulipeca Vol 1. Dirección General de Educación Superior Tecnológica, Instituto Tecnológico de Cd. Victoria, Victoria, Tamaulipas, 2–20.

Anderson KJ (2007) Temporal patterns in rates of community change during succession. The American Naturalist 169: 780–793. https://doi.org/10.1086/516653

Andrews FG, Gilbert AJ (2005) A preliminary annotated checklist and evaluation of the diversity of the Chrysomelidae (Coleoptera) of the Baja California peninsula, Mexico. Insecta Mundi 19: 89–116.

Arroyo-Mora JP, Sánchez-Azofeifa GA, Kalacska MER, Rivard B (2005) Secondary forest detection in a Neotropical dry forest landscape using Landsat 7 ETM+ and IKONOS imagery. Biotropica 37: 497–507. https://doi.org/10.1111/j.1744-7429.2005.00068.x

Aslan EG, Ayvaz Y (2009) Diversity of Alticinae (Coleoptera, Chrysomelidae) in Kasnak Oak Forest Nature Reserve, Isparta, Turkey. Turkish Journal of Zoology 33: 251–262. https://doi.org/10.3906/zoo-0806-2

Bach CE (1981) Host plant growth form and diversity: effects on abundance and feeding preference of a specialist herbivore, *Acalymma vittata* (Coleoptera: Chrysomelidae). Oecologia 50: 370–375. https://doi.org/10.1007/BF00344978

Bach CE (1990) Plant successional stage and insect herbivory: flea beetles on sand-dune willow. Ecology 71: 598–609. https://doi.org/10.2307/1940313

Barberena-Arias MF, Aide TM (2003) Species diversity and trophic composition of litter insects during plant secondary succession. Caribbean Journal of Science 39: 161–169.

Baselga A, Jiménez-Valverde A (2007) Environmental and geographical determinants of beta diversity of leaf beetles (Coleoptera: Chrysomelidae) in the Iberian Peninsula. Ecological Entomology 32: 312–318. https://doi.org/10.1111/j.1365-2311.2007.00880.x

Baselga A, Novoa F (2007) Diversity of Chrysomelidae (Coleoptera) at a mountain range in the limit of the Eurosiberian region, northwest Spain: species richness and beta diversity. Entomologica Fennica 18: 65–73.

Basset Y, Samuelson GA (1996) Ecological characteristics of an arboreal community of Chrysomelidae in Papua New Guinea. In: Jolivet PHA, Cox ML (Eds) Chrysomelidae Biology Volume 2: Ecological Studies. SPB Academic Publishing, Amsterdam, 243–262.

Bongers F, Poorter L, Hawthorne WD, Sheil D (2009) The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. Ecology Letters 12: 798–805. https://doi.org/10.1111/j.1461-0248.2009.01329.x

Bouchard P, Bousquet Y, Davies AE, Alonso-Zarazaga MA, Lawrence JF, Lyal CHC, Newton AF, Reid CAM, Schmitt M, Ślipiński A, Smith ABT (2011) Family-group names in Coleoptera (Insecta). ZooKeys 88: 1–972. https://doi.org/10.3897/zookeys.88.807

Bouchard P, Grebennikov VV, Smith ABT, Douglas H (2009) Biodiversity of Coleoptera. In: Foottit RG, Adler PH (Eds) Insect Biodiversity: Science and Society. Blackwell Publishing, Oxford, 265–301. https://doi.org/10.1002/9781444308211.ch11

Bouzan A, Flinte V, Macedo MV, Monteiro RF (2015) Elevation and temporal distributions of Chrysomelidae in southeast Brazil with emphasis on the Galerucinae. ZooKeys 547: 103–117. https://doi.org/10.3897/zookeys.547.9723

Brown VK, Hyman PS (1986) Successional communities of plants and phytophagous Coleoptera. Journal of Ecology 74: 963–975. https://doi.org/10.2307/2260227

Büchi L, Vuilleumier S (2014) Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. The American Naturalist 183: 612–624. https://doi.org/10.1086/675756

Canizales-Velázquez PA, Alanís-Rodríguez E, Aranda-Ramos R, Mata-Balderas JM, Jiménez-Pérez J, Alanís-Flores G, Uvalle-Sauceda JI, Ruiz-Bautista MG (2009) Caracterización estructural del matorral submontano de la Sierra Madre Oriental, Nuevo León, México. Revista Chapingo Serie Ciencias Forestales y del Ambiente 15: 115–120.

Carignan V, Villard M-A (2002) Selecting indicator species to monitor ecological integrity: a review. Environmental Monitoring and Assessment 78: 45–61. https://doi.org/10.1023/A:1016136723584

Ceballos G, Martínez L, García A, Espinoza E, Creel JB, Dirzo R (2010) Diversidad, amenazas y áreas prioritarias para la conservación de las selvas secas del Pacífico de México. Fondo de Cultura Económica, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, D.F., 594 pp.

Challenger A, Soberón J (2008) Los ecosistemas terrestres. In: CONABIO (Ed.) Capital natural de México, vol I: Conocimiento actual de la biodiversidad. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, 87–108.

Chapin FS, Matson PA, Vitousek PM (2011) Principles of Terrestrial Ecosystem Ecology, Second Edition. Springer Science+Business Media, New York, 529 pp. https://doi.org/10.1007/978-1-4419-9504-9

Chamorro-Lacayo ML (2014) 2.7.5 Chrysomelidae: Cryptocephalinae Gyllenhal 1813. In: Leschen RAB, Beutel RG (Eds) Handbook of Zoology. Arthropoda: Insecta: Coleoptera Volume 3: Morphology and Systematics (Phytophaga). De Gruyter, USA, 81–87.

Chao A, Chiu C-H (2016) Nonparametric estimation and comparison of species richness. John Wiley & Sons Ltd, Chichester, 1–11. https://doi.org/10.1002/9780470015902.a0026329

Charles E, Basset Y (2005) Vertical stratification of leaf-beetle assemblages (Coleoptera: Chrysomelidae) in two forest types in Panama. Journal of Tropical Ecology 21: 329–336. https://doi.org/10.1017/S0266467405002300

Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application. http://purl.oclc.org/estimates

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310. https://doi.org/10.1126/science.199.4335.1302

De-Cáceres M, Legendre P, Wiser SK, Brotons L (2012) Using species combinations in indicator value analyses. Methods in Ecology and Evolution 3: 973–982. https://doi.org/10.1111/j.2041-210X.2012.00246.x

Denslow JS, Guzman GS (2000) Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. Journal of Vegetation Science 11: 201–212. https://doi.org/10.2307/3236800

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:saaist]2.0.co;2

Farrell BD, Erwin TL (1988) Leaf-beetle community structure in an amazonian rainforest canopy. In: Jolivet P, Petitpierre E, Hsiao TH (Eds) Biology of Chrysomelidae. Kluwer Academic Publishers, Dordrecht, 73–90. https://doi.org/10.1007/978-94-009-3105-3_5

Fernandes GW, Almada ED, Carneiro MAA (2010) Gall-inducing insect species richness as indicators of forest age and health. Environmental Entomology 39: 1134–1140. https://doi.org/10.1603/EN09199

Flowers RW (1996) La subfamilia Eumolpinae (Coleoptera: Chrysomelidae) en América Central. Publicación Especial de la Revista de Biología Tropical 2: 1–60.

Flowers RW, Hanson PE (2003) Leaf beetle (Coleoptera: Chrysomelidae) diversity in eight Costa Rican habitats. In: Furth DG (Ed.) Special topics in leaf beetle biology Proceedings of the 5th International Symposium on the Chrysomelidae, Iguassu Falls (Brazil), August 2000. Pensoft Publishers, Sofia-Moscow, 25–51.

Foster BL, Tilman D (2000) Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. Plant Ecology 146: 1–10. https://doi.org/10.1023/A:1009895103017

Furth DG (2013) Diversity of Alticinae in Oaxaca, Mexico: A preliminary study (Coleoptera, Chrysomelidae). ZooKeys 332: 1–32. https://doi.org/10.3897/zookeys.332.4790

García-Morales LJ, Estrada-Castillón AE, García-Jiménez J, Villarreal-Quintanilla JA, Cantú-Ayala C, Jurado-Ybarra E, Vargas-Vázquez VA (2014) Florística y vegetación del Área Natural Protegida Altas Cumbres, Tamaulipas, México. In: Correa-Sandoval A, Horta-Vega JV, García-Jiménez J, Barrientos-Lozano L (Eds) Biodiversidad tamaulipeca Volumen 2,

Número 1. Tecnológico Nacional de México, Instituto Tecnológico de Ciudad Victoria, Tamaulipas, 15–73.

Gómez-Zurita J, Hunt T, Kopliku F, Vogler AP (2007) Recalibrated tree of leaf beetles (Chrysomelidae) indicates independent diversification of angiosperms and their insect herbivores. PLoS ONE 2: e360. https://doi.org/10.1371/journal.pone.0000360

González-Megías A, Gómez JM (2003) Consequences of removing a keystone herbivore for the abundance and diversity of arthropods associated with a cruciferous shrub. Ecological Entomology 28: 299–308. https://doi.org/10.1046/j.1365-2311.2003.00510.x

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. Forest Ecology and Management 148: 185–206. https://doi.org/10.1016/S0378-1127(00)00535-1

Gutman G, Huang C, Chander G, Noojipady P, Masek JG (2013) Assessment of the NASA–USGS Global Land Survey (GLS) datasets. Remote Sensing of Environment 134: 249–265. https://doi.org/10.1016/j.rse.2013.02.026

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4(1): 1–9.

Heusi-Silveira M, Lopes BC, Ide S, Castellani TT, Hernández MIM (2012) Beetle (Insecta, Coleoptera) assemblage in a Southern Brazilian restinga: effects of anthropogenic disturbance and vegetation complexity. Studies on Neotropical Fauna and Environment 47: 203–214. https://doi.org/10.1080/01650521.2012.740258

Hodkinson ID, Jackson JK (2005) Terrestrial and aquatic invertebrates as bioindicators for environmental monitoring, with particular reference to mountain ecosystems. Environmental Management 35: 649–666. https://doi.org/10.1007/s00267-004-0211-x

Hortal J, Borges PAV, Gaspar C (2006) Evaluating the performance of species richness estimators: sensitivity to sample grain size. Journal of Animal Ecology 75: 274–287. https://doi.org/10.1111/j.1365-2656.2006.01048.x

Huston MA (2014) Disturbance, productivity, and species diversity: empiricism vs. logic in ecological theory. Ecology 95: 2382–2396. https://doi.org/10.1890/13-1397.1

INEGI (2013) Conjunto de datos vectoriales de uso del suelo y vegetación escala 1:250,000, Serie V (Capa Unión). Aguascalientes, México: Instituto Nacional de Estadística y Geografía.

Janzen DH (1976) Sweep samples of tropical deciduous forest foliage-inhabiting insects: seasonal changes and inter-field differences in adult bugs and beetles. Revista de Biología Tropical 24: 149–161.

Jeffries JM, Marquis RJ, Forkner RE (2006) Forest age influences oak insect herbivore community structure, richness, and density. Ecological Applications 16: 901–912. https://doi.org/10.1890/1051-0761(2006)016[0901:FAIOIH]2.0.CO;2

Jiménez-Valverde A, Hortal J (2003) Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. Revista Ibérica de Aracnología 8: 151–161.

Johnson EA, Miyanishi K (2008) Testing the assumptions of chronosequences in succession. Ecology Letters 11: 419–431. https://doi.org/10.1111/j.1461-0248.2008.01173.x

Jolivet P (1988) Food habits and food selection of Chrysomelidae: bionomic and evolutionary perspectives. In: Jolivet P, Petitpierre E, Hsiao TH (Eds) Biology of Chrysomelidae. Kluwer Academic Publishers, Dordrecht, 1–24. https://doi.org/10.1007/978-94-009-3105-3_1

Jolivet P (2015) Together with 30 years of Symposia on Chrysomelidae! Memories and personal reflections on what we know more about leaf beetles. Zookeys 547: 35–61. https://doi.org/10.3897/zookeys.547.7181

Jolivet P, Verma KK (2008) Eumolpinae – a widely distributed and much diversified subfamily of leaf beetles (Coleoptera, Chrysomelidae). Terrestrial Arthropod Reviews 1: 3–37. https://doi.org/10.1163/187498308X345424

Jost L (2006) Entropy and diversity. Oikos 113: 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Kalaichelvan T, Verma KK (2005) Checklist of leaf beetles (Coleoptera: Chrysomelidae) of Bhilai-Durg. Zoos' Print Journal 20: 1838–1842. https://doi.org/10.11609/JoTT.ZPJ.1114.1838-42

Lebrija-Trejos E, Pérez-García EA, Meave JA, Poorter L, Bongers F (2011) Environmental changes during secondary succession in a tropical dry forest in Mexico. Journal of Tropical Ecology 27: 477–489. https://doi.org/10.1017/S0266467411000253

Linzmeier AM, Ribeiro-Costa CS (2009) Spatio-temporal dynamics of Alticini (Coleoptera, Chrysomelidae) in a fragment of araucaria forest in the state of Parana, Brazil. Revista Brasileira de Entomologia 53: 294–299. https://doi.org/10.1590/S0085-56262009000200013

Linzmeier AM, Ribeiro-Costa CS (2011) Body size of Chrysomelidae (Coleoptera, Insecta) in areas with different levels of conservation in south Brazil. ZooKeys 157: 1–14. https://doi.org/10.3897/zookeys.157.1083

Linzmeier AM, Ribeiro-Costa CS (2012) Spatial–temporal composition of Chrysomelidae (Insecta: Coleoptera) communities in southern Brazil. Journal of Natural History 46(31–32): 1921–1938. https://doi.org/10.1080/00222933.2012.707237

Linzmeier AM, Ribeiro-Costa CS (2013) Seasonal pattern of Chrysomelidae (Coleoptera) in the state of Paraná, southern Brazil. Biota Neotropica 13(1): 1–10. https://doi.org/10.1590/S1676-06032013000100018

Linzmeier AM, Ribeiro-Costa CS, Marinoni RC (2006) Fauna de Alticini (Newman) (Coleoptera, Chrysomelidae, Galerucinae) em diferentes estágios sucessionais na Floresta com Araucária do Paraná, Brasil: diversidade e estimativa de riqueza de espécies. Revista Brasileira de Entomologia 50: 101–109. https://doi.org/10.1590/S0085-56262006000100015

Lucio-García JN (2018) Efecto de la estacionalidad y el microclima sobre Chrysomelidae (Coleoptera) en un bosque tropical subcaducifolio de Victoria, Tamaulipas. Bachelor thesis, Tamaulipas, México: Universidad Autónoma de Tamaulipas.

Magurran AE (2004) Measuring biological diversity. Blackwell Science Ltd., Oxford, 256 pp.

Marinoni RC, Ganho NG (2006) A diversidade diferencial beta de Coleoptera (Insecta) em uma paisagem antropizada. Revista Brasileira de Entomologia 50: 64–71. https://doi.org/10.1590/S0085-56262006000100009

Martínez-Sánchez I, Niño-Maldonado S, Barrientos-Lozano L, Horta-Vega JV (2009) Dinámica poblacional de Chrysomelidae (Coleoptera) en un gradiente altitudinal en tres municipios del estado de Hidalgo, México. TecnoINTELECTO 6: 2–4.

McGeoch MA, Rensburg BJV, Botes A (2002) The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. Journal of Applied Ecology 39: 661–672. https://doi.org/10.1046/j.1365-2664.2002.00743.x

Morrone JJ, Márquez J (2008) Biodiversity of Mexican terrestrial arthropods (Arachnida and Hexapoda): a biogeographical puzzle. Acta Zoológica Mexicana (ns)24: 15–41. https://doi.org/10.21829/azm.2008.241613

Morrow PA, Tonkyn DW, Goldburg RJ (1989) Patch colonization by *Trirhabda canadensis* (Coleoptera: Chrysomelidae): effects of plant species composition and wind. Oecologia 81: 43–50. https://doi.org/10.1007/BF00377008

Myster RW, Malahy MP (2008) Is there a middle way between permanent plots and chronosequences? Canadian Journal of Forest Research 38: 3133–3138. https://doi.org/10.1139/X08-148

Niño-Maldonado S, Riley EG, Furth DG, Jones RW (2005) Coleoptera: Chrysomelidae. In: Sánchez-Ramos G, Reyes-Castillo P, Dirzo R (Eds) Historia Natural de la Reserva de la Biósfera El Cielo, Tamaulipas, México. Universidad Autónoma de Tamaulipas, Victoria, 417–425.

Niño-Maldonado S, Romero-Nápoles J, Sánchez-Reyes UJ, Jones RW, De-León-González EI (2014) Inventario preliminar de Chrysomelidae (Coleoptera) de Tamaulipas, México. In: Correa-Sandoval A, Horta-Vega JV, García-Jiménez J, Barrientos-Lozano L (Eds) Biodiversidad Tamaulipeca Volumen 2, Número 2. Tecnológico Nacional de México, Instituto Tecnológico de Cd. Victoria, Tamaulipas, 121–132.

Niño-Maldonado S, Sánchez-Reyes UJ (2017) Taxonomía de insectos. Orden Coleoptera. Familia Chrysomelidae. In: Cibrián-Tovar D (Ed.) Fundamentos de entomología forestal. Red de salud forestal. Redes temáticas de la Comisión Nacional de Ciencia y Tecnología (CONACYT), México, 282–288.

Nummelin M, Borowiec L (1992) Cassidinae beetles of the Kibale Forest, western Uganda; comparison between virgin and managed forests. African Journal of Ecology 30: 10–17. https://doi.org/10.1111/j.1365-2028.1992.tb00474.x

O'Brien MJ, Brezzi M, Schuldt A, Zhang J-Y, Ma K, Schmid B, Niklaus PA (2017) Tree diversity drives diversity of arthropod herbivores, but successional stage mediates detritivores. Ecology and Evolution 7: 8753–8760. https://doi.org/10.1002/ece3.3411

Ordóñez-Reséndiz MM, Serrano-Resendiz V, Hernández-Sosa L (2015) Riqueza de la familia Chrysomelidae (Coleoptera) en comunidades vegetales de las Sierras de Taxco-Huautla. Entomología Mexicana 2: 601–607.

Pellissier L (2015) Stability and the competition-dispersal trade-off as drivers of speciation and biodiversity gradients. Frontiers in Ecology and Evolution 3: 1–10. https://doi.org/10.3389/fevo.2015.00052

Perry J, Lojka B, Ruiz LQ, Damme PV, Houška J, Cusimamani EF (2016) How natural forest conversion affects insect biodiversity in the Peruvian Amazon: can agroforestry help? Forests 7: 1–13. https://doi.org/10.3390/f70400822

Pickett STA, Cadenasso ML, Meiners SJ (2008) Ever since Clements: from succession to vegetation dynamics and understanding to intervention. Applied Vegetation Science 12: 9–21. https://doi.org/10.1111/j.1654-109X.2009.01019.x

Pimenta M, De-Marco P (2015) Leaf beetle (Chrysomelidae: Coleoptera) assemblages in a mosaic of natural and altered areas in the Brazilian Cerrado. Neotropical Entomology 44: 242–255. https://doi.org/10.1007/s13744-015-0280-y

Pulsford SA, Lindenmayer DB, Driscoll DA (2016) A succession of theories: purging redundancy from disturbance theory. Biological Reviews 91: 148–167. https://doi.org/10.1111/brv.12163

Řehounek J (2002) Comparative study of the leaf beetles (Coleoptera: Chrysomelidae) in chosen localities in the district of Nymburk. Acta Universitatis Palackianae Olomucensis Facultas Rerum Naturalium Biologica 39–40: 123–130.

Ribera I, Foster G (1997) El uso de artrópodos como indicadores biológicos. Boletín de la Sociedad Entomológica Aragonesa 20: 265–276.

Riley EG, Clark SM, Flowers RW, Gilbert AJ (2002) 124 Chrysomelidae Latreille 1802. In: Arnett RH, Thomas MC, Skelley PE, Frank JH (Eds) Volume 2, American Beetles. Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press LLC, USA, 617–691.

Riley EG, Clark SM, Seeno TN (2003) Catalog of the Leaf Beetles of America North of Mexico. Coleopterists Society, special publication no. 1, 290 pp.

Roxburgh SH, Shea K, Wilson JB (2004) The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. Ecology 85: 359–371. https://doi.org/10.1890/03-0266

Rzedowski J (2006) Vegetación de México. 1ra. Edición digital. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, 504 pp.

Sánchez-Reyes UJ, Niño-Maldonado S, Barrientos-Lozano L, Clark SM, Jones RW (2016) Faunistic patterns of leaf beetles (Coleoptera, Chrysomelidae) within elevational and temporal gradients in Sierra de San Carlos, Mexico. ZooKeys 611: 11–56. https://doi.org/10.3897/zookeys.611.9608

Sánchez-Reyes UJ, Niño-Maldonado S, Barrientos-Lozano L, Jones RW, Sandoval-Becerra FM (2015) Análisis del nicho ecológico de Cryptocephalinae (Coleoptera: Chrysomelidae) en la Sierra de San Carlos, Tamaulipas, México. Entomología Mexicana 2: 526–532.

Sánchez-Reyes UJ, Niño-Maldonado S, Barrientos-Lozano L, Treviño-Carreón J (2017) Assessment of land use-cover changes and successional stages of vegetation in the Natural Protected Area Altas Cumbres, Northeastern Mexico, using Landsat satellite imagery. Remote Sensing 9: 1–33. https://doi.org/10.3390/rs9070712

Sánchez-Reyes UJ, Niño-Maldonado S, Barrientos-Lozano L, Treviño-Carreón J, Almaguer-Sierra P (in press) Seasonal microclimatic variation in a succession gradient of low thorn forest in Northeastern Mexico. Revista de Biología Tropical.

Sánchez-Reyes UJ, Niño-Maldonado S, Jones RW (2014) Diversity and altitudinal distribution of Chrysomelidae (Coleoptera) in Peregrina Canyon, Tamaulipas, Mexico. ZooKeys 417: 103–132. https://doi.org/10.3897/zookeys.417.7551

Sandoval-Becerra FM (2018) Ensamble de Chrysomelidae (Coleoptera) en un mosaico de disturbio dentro del Área Natural Protegida Altas Cumbres, Victoria, Tamaulipas. MSc thesis, Tamaulipas, México: Tecnológico Nacional de México, Instituto Tecnológico de Ciudad Victoria.

Sandoval-Becerra FM, Niño-Maldonado S, Sánchez-Reyes UJ, Horta-Vega JV, Venegas-Barrera CS, Martínez-Sánchez I (2017) Respuesta de la comunidad de Chrysomelidae (Coleoptera) a la variación microclimática en un fragmento de bosque de encino del noreste de México. Entomología Mexicana 4: 420–426.

Sandoval-Becerra FM, Sánchez-Reyes UJ, Clark SM, Venegas-Barrera CS, Horta-Vega JV, Niño-Maldonado S (2018) Influence of habitat heterogeneity on structure and composition of a Chrysomelidae (Coleoptera) assemblage in a temperate forest in northeast Mexico. Southwestern Entomologist 43: 115–130. https://doi.org/10.3958/059.043.0129

Scherer G (1983) Diagnostic key for the Neotropical Alticinae genera. Entomologische Arbeiten aus dem Museum G Frey 31–32: 2–89.

Secretaría de Gobierno (2015) Decreto Gubernamental mediante el cual se aprueba el Programa de Manejo del Área Natural Protegida "Altas Cumbres", localizada en los municipios de Jaumave y Victoria, Tamaulipas. Órgano del Gobierno Constitucional del Estado Libre y Soberano de Tamaulipas, Periódico Oficial del Estado de Tamaulipas, Tomo CXL, Secretaría General de Gobierno, Ciudad Victoria, Tamaulipas.

Şen I, Gök A (2009) Leaf beetle communities (Coleoptera: Chrysomelidae) of two mixed forest ecosystems dominated by pine-oak-hawthorn in Isparta province, Turkey. Annales Zoologici Fennici 46: 217–232. https://doi.org/10.5735/086.046.0306

Şen İ, Gök A (2014) Leaf beetle (Coleoptera: Chrysomelidae) communities of Kovada Lake and Kızıldağ national parks (Isparta, Turkey): assessing the effects of habitat types. Entomological Research 44: 176–190. https://doi.org/10.1111/1748-5967.12064

Shea K, Roxburgh SH, Rauschert ESJ (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecology Letters 7: 491–508. https://doi.org/10.1111/j.1461-0248.2004.00600.x

Staines CL (1986) A revision of the genus *Brachycoryna* (Coleoptera: Chrysomelidae: Hispinae). Insecta Mundi 1(4): 231–241.

Staines CL (2002) The New World tribes and genera of hispines (Coleoptera: Chrysomelidae: Cassidinae). Proceedings of the Entomological Society of Washington 104(3): 721–784.

Staines CL, Staines SL (2001) The leaf beetles (Insecta: Coleoptera: Chrysomelidae): potential indicator species assemblages for natural area monitoring. In: Therres GD (Ed.) Proceedings of conservation of biological diversity: a key to restoration of the Chesapeake Bay ecosystem and beyond. Maryland Department of Natural Resources, Maryland, 233–244.

StatSoft (2007) STATISTICA, version 8.0. http://www.statsoft.com

Steffan-Dewenter I, Tscharntke T (2001) Succession of bee communities on fallows. Ecography 24: 83–93. https://doi.org/10.1034/j.1600-0587.2001.240110.x

Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17: 866–880. https://doi.org/10.1111/ele.12277

Stephen C, Sánchez R (2014) Species richness and relative species abundance of Nymphalidae (Lepidoptera) in three forests with different perturbations in the north-central Caribbean of Costa Rica. Revista de Biología Tropical 62: 919–928. https://doi.org/10.15517/rbt.v62i3.14057

Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, DellaSala DA, Hutto RL, Lindenmayer DB, Swanson FJ (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9: 117–125. https://doi.org/10.1890/090157

Tamme R, Hiiesalu I, Laanisto L, Szava-Kovats R, Pärtel M (2010) Environmental heterogeneity, species diversity and co-existence at different spatial scales. Journal of Vegetation Science 21: 796–801. https://doi.org/10.1111/j.1654-1103.2010.01185.x

Tejeda-Cruz C, Mehltreter K, Sosa VJ (2008) Indicadores ecológicos multi-taxonómicos. In: Manson RH, Hernández-Ortiz V, Gallina S, Mehltreter K (Eds) Agroecosistemas cafetaleros de Veracruz: biodiversidad, manejo y conservación. Instituto Nacional de Ecología A. C., México, 271–278.

Trejo I (2010) Las selvas secas del Pacífico mexicano. In: Ceballos G, Martínez L, García A, Espinoza E, Creel JB, Dirzo R (Eds) Diversidad, amenazas y áreas prioritarias para la conservación de las selvas secas del Pacífico de México. Fondo de Cultura Económica, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, D.F., México, 41–51.

Treviño-Carreón J, Valiente-Banuet A (2005) La vegetación de Tamaulipas y sus principales asociaciones vegetales. In: Barrientos-Lozano L, Correa-Sandoval A, Horta-Vega JV, García-Jiménez J (Eds) Biodiversidad tamaulipeca Vol 1. Dirección General de Educación Superior Tecnológica, Instituto Tecnológico de Ciudad Victoria, Ciudad Victoria, Tamaulipas, México, 22–46.

Vieira ICG, Almeida ASd, Davidson EA, Stone TA, Carvalho CJRd, Guerrero JB (2003) Classifying successional forests using Landsat spectral properties and ecological characteristics in eastern Amazonia. Remote Sensing of Environment 87: 470–481. https://doi.org/10.1016/j.rse.2002.09.002

Villa-Galaviz E, Boege K, Del-Val E (2012) Resilience in plant-herbivore networks during secondary succession. PLoS ONE 7: e53009. https://doi.org/10.1371/journal.pone.0053009

Walker LR, Wardle DA, Bardgett RD, Clarkson BD (2010) The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98: 725–736. https://doi.org/10.1111/j.1365-2745.2010.01664.x

Wąsowska M (2004) Impact of humidity and mowing on chrysomelid communities (Coleoptera, Chrysomelidae) in meadows of the Wierzbanówka valley (Pogórze Wielickie hills, Southern Poland). Biologia Bratislava 59: 601–611.

White RE (1968) A review of the genus *Cryptocephalus* in America north of Mexico (Chrysomelidae: Coleoptera). United States National Museum Bulletin 290: 1–124. https://doi.org/10.5479/si.03629236.290.1

White RE (1993) A revision of the subfamily Criocerinae (Chrysomelidae) of North America north of Mexico. Technical Bulletin 1805. United States Department of Agriculture, Agricultural Research Service, Washington, DC, 158 pp.

Wilcox JA (1965) A synopsis of the North American Galerucinae (Coleoptera: Chrysomelidae). New York State Museum and Science Service Bulletin 400: 1–226.

Wilcox JA (1972) A review of the North American Chrysomelinae leaf beetles (Coleoptera: Chrysomelidae). Bulletin 421. University of the State of New York, State Education Department, State Museum and Science Service, 37 pp.

Willig MR, Presley SJ (2018) Biodiversity and disturbance. In: DellaSala DA, Goldstein MI (Eds) The Encyclopedia of the Anthropocene, vol 3. Elsevier, Oxford, 45–51. https://doi.org/10.1016/B978-0-12-809665-9.09813-X

Winter M-B, Ammer C, Baier R, Donato DC, Seibold S, Müller J (2015) Multi-taxon alpha diversity following bark beetle disturbance: Evaluating multi-decade persistence of a diverse early-seral phase. Forest Ecology and Management 338: 32–45. https://doi.org/10.1016/j.foreco.2014.11.019

Yang Z, Liu X, Zhou M, Ai D, Wang G, Wang Y, Chu C, Lundholm JT (2015) The effect of environmental heterogeneity on species richness depends on community position along the environmental gradient. Scientific Reports 5: 1–7. https://doi.org/10.1038/srep15723

Yuan ZY, Jiao F, Li YH, Kallenbach RL (2016) Anthropogenic disturbances are key to maintaining the biodiversity of grasslands. Scientific Reports 6: 1–8. https://doi.org/10.1038/srep22132

Appendix I

Table 7. Taxonomic checklist of Chrysomelidae per season in each category of succession time, in a fragment of low thorn forest in northeastern Mexico. Key: 4y = 4 years of succession, 17y = 17 years of succession, 31y = 31 years of succession, CA = Conserved areas.

Species	Rainy season				Dry season			
	4y	17y	31y	CA	4y	17y	31y	CA
CRIOCERINAE Latreille, 1807								
Tribe Lemini Heinze, 1962								
Lema sp. 1								1
Lema sp. 2							1	
Oulema sp. 1 *	1							
Neolema sp. 1	1							
CASSIDINAE Gyllenhal, 1813								
Tribe Chalepini Weise, 1910								
Baliosus sp. 1	2		4	3		2		
Brachycoryna pumila Guérin-Méneville, 1844	33				30	8		
Chalepus amabilis Baly 1885								3
Chalepus bellulus (Chapuis, 1877)	3							
Chalepus digressus Baly 1885				2				
Heterispa vinula (Erichson, 1847)	21	50	23	7	15	43	21	
Pentispa distincta (Baly 1885)								2
Sumitrosis inaequalis (Weber, 1801)	1	1	4			2	7	
Tribe Ischyrosonychini Chapuis, 1875								
Physonota alutacea Boheman, 1854		6	3			4		
Tribe Cassidini Gyllenhal, 1813								
Agroiconota vilis (Boheman, 1855)					1			
Charidotella bifossulata (Boheman, 1855)								1
Charidotella sexpunctata (Fabricius, 1781)	2			2			3	3
Charidotis auroguttata Boheman, 1855				4				
Helocassis clavata (Fabricius, 1798)	3	1		17	2	3	2	9
CHRYSOMELINAE Latreille, 1802								
Tribe Chrysomelini Latreille, 1802								
Subtribe Doryphorina Motschulsky, 1860								
Calligrapha ancoralis Stål, 1860	10	1						
Calligrapha piceicollis Stål, 1859	1				2			
Deuterocampta atromaculata Stål, 1859)		1	3	2			2	
Subtribe Chrysomelina Latreille, 1802								
Plagiodera semivittata Stål, 1860		1					3	
Plagiodera thymaloides Stål, 1860	8	1	8		8		3	
GALERUCINAE Latreille, 1802								
Tribe Galerucini Latreille, 1802								
Group Coelomerites Chapuis, 1875								
Coraia subcyanescens (Schaeffer, 1906)		3	1	1				
Derospidea ornata (Schaeffer, 1905)			2					
Miraces aeneipennis Jacoby, 1888								1
Tribe Luperini Chapuis, 1875								
Subtribe Diabroticina Chapuis, 1875								
Group Diabroticites Chapuis, 1875								
Diabrotica litterata Sahlberg 1823	8			4	2			
Group Cerotomites Chapuis, 1875								
Cyclotrypema furcata (Olivier, 1808)	31	32	3		7	20		
Tribe Alticini Newman, 1835								
Acallepitrix sp. 1		4	1	8		2		4

Species	Rainy season				Dry season			
	4y	17y	31y	CA	4y	17y	31y	CA
Acallepitrix sp. 2				5				
Acrocyum dorsalis Jacoby, 1885				11				4
Alagoasa bipunctata (Chevrolat, 1834)		4	4	9				2
Alagoasa jacobiana (Horn, 1889)	5		6	17		4		10
Alagoasa sp. 1						1		
Alagoasa sp. 2	2							
Asphaera sp. 1	7	1			3			
Centralaphthona diversa (Baly, 1877)	280	1172	1261	167	103	240	217	18
Chaetocnema sp. 1	976	61			41	8		2
Chaetocnema sp. 2	1				3			2
Dibolia sp. 1				1				
Disonycha glabrata (Fabricius, 1781)	4	1		1				
Disonycha sp. 2					16			
Disonycha stenosticha Schaeffer, 1931			2	1				
Dysphenges sp. 1	14	13	25	2			2	
Epitrix sp. 1	287	1	1	44	320	3		12
Epitrix sp. 2	16	3	3	25		4		21
Epitrix sp. 3	183	7		27	41		2	
Epitrix sp. 4	5	1		16	4			20
Epitrix sp. 5	1	2		4	2	2		8
Heikertingerella sp. 1				3				
Longitarsus sp. 1	32	10	10	40	7	4		8
Macrohaltica jamaicensis (Fabricius, 1792)	1							
Margaridisa sp. 1	46		21	80	8	3	8	152
Margaridisa sp. 2								4
Monomacra bumeliae (Schaeffer, 1905)	4	3		3		2		
Omophoita cyanipennis (Fabricius, 1798)					3			
Parchicola sp. 1				11	2			6
Parchicola sp. 2	6							
Parchicola sp. 3				1				
Syphrea sp. 1	2			1				
Syphrea sp. 2								2
Syphrea sp. 3	3							
Systena sp. 1					1			
EUMOLPINAE Hope, 1840								
Tribe Eumolpini Hope, 1840								
Group Iphimeites Chapuis, 1874								
Brachypnoea sp. 1	4							
Colaspis melancholica Jacoby, 1881				3				
Colaspis sp. 1	1							
Colaspis townsendi Bowditch, 1921	20	1		5	15			
Zenocolaspis inconstans (Lefèvre, 1878)	3		2	2	3			
Tribe Typophorini Chapuis, 1874								
Group Typophorites Chapuis, 1874								
Paria sp. 1			1	1				
CRYPTOCEPHALINAE Gyllenhal, 1813								
Tribe Cryptocephalini Gyllenhal, 1813								
Subtribe Pachybrachina Chapuis, 1874								
Pachybrachis sp. 1	5	1			2	4		
Pachybrachis sp. 2	1				4			
Pachybrachis sp. 3	3	1					4	
Pachybrachis sp. 4	3	2			4		2	
Pachybrachis sp. 5	1							
Pachybrachis sp. 6	1							

Species	Rainy season				Dry season			
	4y	17y	31y	CA	4y	17y	31y	CA
Subtribe Cryptocephalina Gyllenhal, 1813								
Cryptocephalus guttulatus Olivier,1808	1							
Cryptocephalus trizonatus Suffrian, 1858	3				4			
Diachus sp. 1			2					
Tribe Clytrini Lacordaire, 1848								
Subtribe Clytrina Lacordaire, 1848								
Anomoea rufifrons mutabilis (Lacordaire, 1848)	1	1						
Smaragdina agilis (Lacordaire, 1848)					2			
Subtribe Ischiopachina Chapuis, 1874								
Ischiopachys bicolor proteus Lacordaire, 1848	5		1					
Subtribe Babiina Chapuis, 1874								
Babia tetraspilota texana Schaeffer, 1933	10	3	6	1	4	2		
Subtribe Megalostomina Chapuis, 1874								
Proctophana sp. 1					1			
Tribe Fulcidacini Jakobson, 1924								
Chlamisus sp. 1	1							
Diplacaspis prosternalis (Schaeffer, 1906)	2	1				2		